J. Physiol. (1973), **233**, *pp.* 575–588
With 2 plates and 4 text-figures
Printed in Great Britain

RETENTION OF THE ORIGINAL TOPOGRAPHIC POLARITY BY THE 180° ROTATED TECTAL REIMPLANT IN YOUNG ADULT GOLDFISH

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(*Received 6 March 1973*)

SUMMARY

1. The pattern of visual projection from the retina on to the optic tectum was studied with neurophysiological mapping methods following reimplantation of the optic tectum in young adult goldfish.

2. When a rectangular piece of the tectum was dissected out and then reimplanted to the same tectum *in situ*, the restored visual projection showed a normal retinotopic order over the area of the tectal reimplant.

3. If the tectal tissue was reimplanted after rotation by 180°, the visual projection from that part of the retina which innervated the 180° rotated tectal reimplant was found to be organized in a completely reverse retinotopic order within the reimplanted area in contrast to the normal projection from the other part of the retina on to the intact surrounding area of the same optic tectum.

4. The results indicate that a piece of reimplanted tectal tissue retains its original topographic polarity regardless of whether the tectal tissue was rotated or not.

5. The retention of original topographic polarity by a small fraction of the tectal tissue suggests that the optic tectum is not a passive receiver of incoming optic fibres but an active accommodator which selects appropriate optic fibres to make proper synaptic connexions in a consistent topographic order.

INTRODUCTION

During embryonic development of the visual system, many hundred thousands of axons sprout out from ganglion cells in the retina and then preferentially select particular routes to their appropriate destinations to make functional connexions with the mid-brain visual centres in a consistent topographical order. To account for this orderly development of specific neural connexions Sperry (1943*a*, *b*, 1944, 1945, 1948, 1963, 1965)

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proposed a chemoaffinity hypothesis of neuronal specificity, which postulates three basic developmental events. (I) Topographical polarization of the retina: ganglion cells in the optic cup undergo a polarized field or gradient type of embryonic differentiation along the nasotemporal and the dorsoventral axes, and acquire differential affinities (of cytochemical nature) for intercellular recognitions according to their locations in the retinal field. (II) Topographical polarization of the optic tectum: visual neurones in the optic tectum also undergo congruent embryonic differentiation and acquire matching or complementary affinities according to their positions in the tectal field. (III) Selective formation of synapses on the basis of chemoaffinities: the ingrowing axons of the ganglion cells are guided chemotactically to appropriate zones in the tectum and preferentially form synaptic connexions with selected tectal neurons with matching or complementary cytochemical affinities.

The topographical polarization of the retina has been investigated in a number of experiments involving rotation of the eye anlage at various stages of embryonic development in lower vertebrates. Stone (1944, 1947, 1948, 1953, 1960) found in salamander (*Amblystoma punctatum*) that the topographical polarization of the retina occurred at an early embryonic stage in the development (Harrison stage 36) while the neural elements of the rapidly proliferating retina had not morphologically differentiated as yet, and, thus, much earlier than the outgrowth of axons from ganglion cells; if the optic cups were excised, rotated 180° and then reimplanted or transplanted to hosts after the critical embryonic stage, these hosts later developed consistently inverted visuomotor responses whereas the other hosts whose reimplanted eyes had been rotated 180° before the critical stage showed later normal vision regardless of the eye rotation. Székely (1954) observed in newt (*Triturus taeniatum*) that the retina became polarized along the nasotemporal axis first as predicted by Sperry (1943*b*) and then along the dorsoventral axis. The same trends have been also confirmed in toad (*Xenopus laevis*) by Jacobson (1967, 1968*a*, *b*) and Hunt & Jacobson (1972) in a series of experiments with refined electrophysiological mapping methods.

On the other hand, the topographic polarization of the optic tectum has not been well explored experimentally as yet. Crelin (1952) reported that when the presumptive optic tectum was rotated 180° in *Ambystoma* at an early embryonic stage (Harrison stage 31) before the retinal polarization became fixed, the animal later showed normal vision. When the tectum was reimplanted at a later stage, however, the grafted tectal tissue did not survive. This technical difficulty made it impossible for Crelin to test whether the optic tectum underwent a topographical polarization or not. Recently, however, Gaze, Jacobson & Sharma (1966) reported that when

a part of the optic tectum was excised and then reimplanted *in situ* in adult goldfish, the reimplanted tectal tissue became reinnervated by optic fibres and the retinotectal projection was restored to near normal over the area of the tectal reimplant. In the present experiments tectal reimplants were rotated by 180° in adult goldfish to test for topographic polarization of the optic tectum and whether the rotated tissue would retain its original polarity. Prior to completion of the present work, Sharma & Gaze (1971) succeeded in similar experiments involving rotation of tectal grafts by 90° in adult goldfish. A preliminary account of the present results was presented (Yoon, 1972*a*).

METHODS

Goldfish (*Crassius auratus*) used in the present experiments were about 11–17 months old and about 7·5–8·5 cm long from the nose to the base of tail at the time of surgery. Before either surgery or neurophysiological recording, individual fish were anaesthetized by immersion in either 5% ethyl carbamate or in 0·03% tricaine methane sulphonate (MS 222. Ayerst Lab. Inc.) for 2–5 min and then placed between two soft sponge pads that restrained the fish to a desired position within a plastic holder. The gills were continually infused with aerated water through a tube in the mouth. The rate of infusion was adjustable to any value between 0 and 1200 ml./min.

The experiments involved the following types of surgical operations. (*a*) A rectangular piece of the tectal tissue was dissected out from near the central zone of the dorsal tectum by making deep incisions with microscissors and microforceps down to the level of the optic ventricle. (*b*) The dissected piece of tectal tissue was lifted free and then reimplanted to the same optic tectum either *in situ* (Pl. 1*a*), or after a rotation by 180° (Pl. 1*b*). The area of the tectal reimplant ranged from about one sixth to one fourth of the dorsal surface of the optic tectum. (*c*) Complete cut of optic fibres within the sheath of optic nerve by squeezing and teasing with finely pointed forceps at a distance of about 1 mm from the posterior pole of the eyeball. Only one tectum was exposed at a time by opening a single cranial bone flap that was restored at the completion of surgery. All surgeries and neurophysiological recordings were performed with the aid of a stereomicroscope at magnifications of 6–40 times.

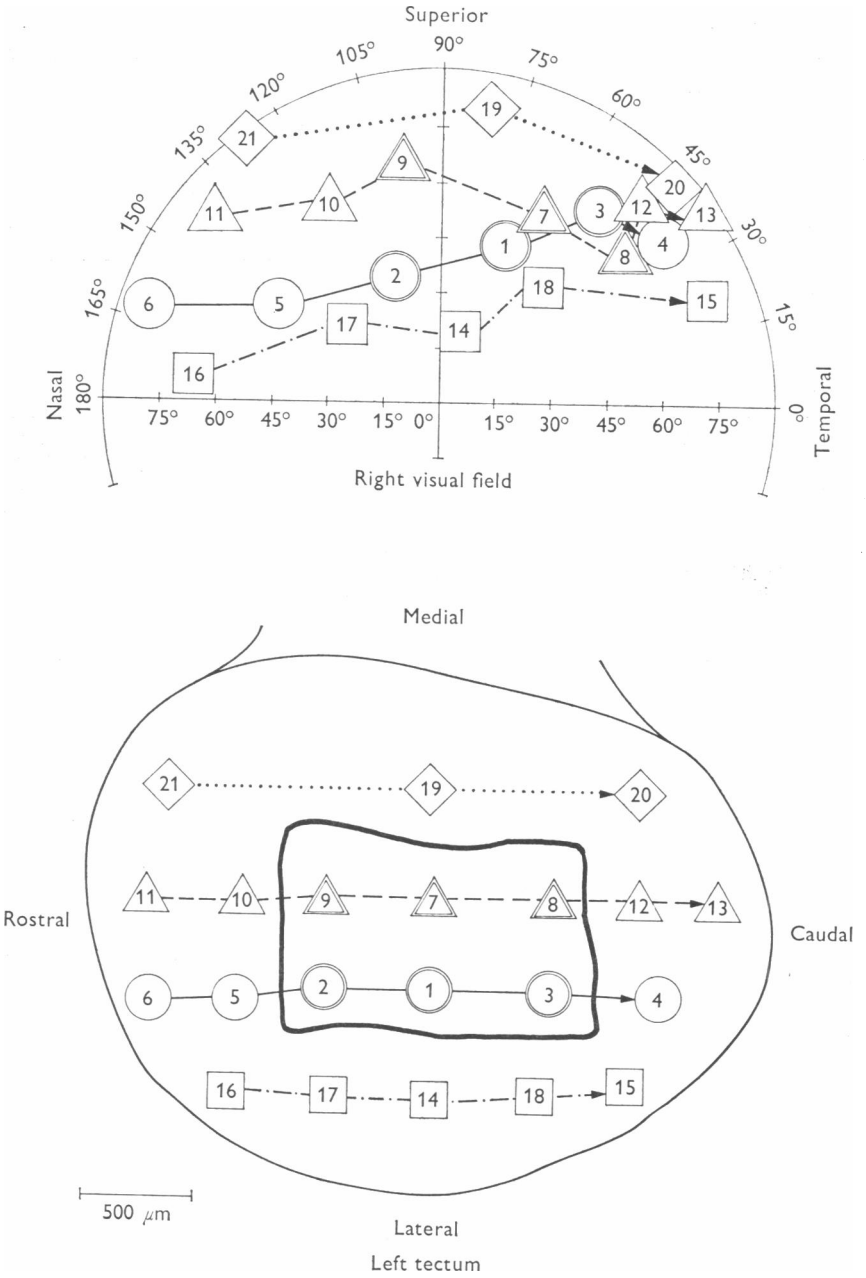
Standard neurophysiological methods were used for mapping retinotectal projection as fully described in previous reports (Yoon, 1971, 1972*b*). In brief, action potentials were recorded with tungsten micro-electrodes from various locations on the dorsal tectum, and then the corresponding receptive fields for the tectal units were marked on the perimetric chart of the contralateral visual field. The locations of recording micro-electrodes were marked on a polaroid picture of the optic tectum at a magnification of 40 times.

At the end of a neurophysiological mapping session the brain was fixed in Bodian fixative, embedded in paraffin and serially sectioned at 15 μm. These sections of the brain were stained by the Bodian protargol method.

RESULTS

Retinal projection on to tectal reimplant in situ

Experiment 1. In twenty-four fish a rectangular piece of the tectal tissue was dissected out from near the central zone of the left tectum,



Text-fig. 1. For legend see facing page.

lifted free, and then reimplanted in its original position (Pl. 1*a*). Optic nerves were left intact in twelve fish whereas the right optic nerve was sectioned and allowed to regenerate in the other twelve fish. About 2 months after the surgery, these fish suffered widespread bacterial skin infections, and only seven fish survived up to 6 months. Retinotectal projections were mapped at intervals between 67 and 172 days after the tectal reimplantation. In four of the seven fish, the reimplanted tectal tissue was found to be missing from the optic tectum which showed a transparent rectangular hollow near the central zone of its dorsal surface (Pl. 1*c*). In the case of the other three fish, however, the tectal reimplant was found in place, and furthermore it gave neural responses to visual stimuli. Text-fig. 1 shows a retinotectal projection map obtained 172 days after the tectal reimplantation combined with section of the contralateral optic nerve. In spite of a few minor errors, the map indicates that the newly reestablished visual projection restored a more or less normal topographic pattern within the area of the tectal reimplant as well as over the intact surrounding area of the tectum. In the other two fish the tectal reimplant *in situ* was found to have been reinnervated by regenerating optic fibres in essentially correct retinotopic order.

The present result confirms previous findings (Gaze *et al.* 1966; Sharma & Gaze, 1971) that the tectal tissue of goldfish may survive excision and reimplantation even in adulthood (about $1\frac{1}{2}$ yr old), and that such reimplants eventually become reinnervated by appropriate optic fibres. This extraordinary property of the goldfish optic tectum makes it possible to test whether the topographic polarization of the optic tectum became fixed so that the tectal reimplant retains its original polarity after rotation.

Text-fig. 1. Projection of the visual field on to the contralateral optic tectum following reimplantation of a rectangular piece of tectal tissue to the same tectum *in situ*. The numbers marked on the enlarged drawing of the tectum indicate the positions of recording sites on the dorsal surface of the tectum in the order of their recordings of visual responses with micro-electrodes. The corresponding numbers marked on the perimetric chart show the locations of the corresponding receptive fields in the contralateral visual field for the experimental points on the tectum. The retinotectal projection map, obtained 172 days after the tectal reimplantation *in situ*, shows more or less normal topographical pattern: A nasotemporal series in the visual field is represented by a rostrocaudal series on the tectum whereas a dorsoventral series in the upper half of the visual field is represented by a mediolateral series on the tectum (except the errors caused by the points 3 and 8 on the tectal reimplant). No attempts were made to record from the curled ventrolateral surface of the rectum which is known to receive projections from the lower half of the visual field.

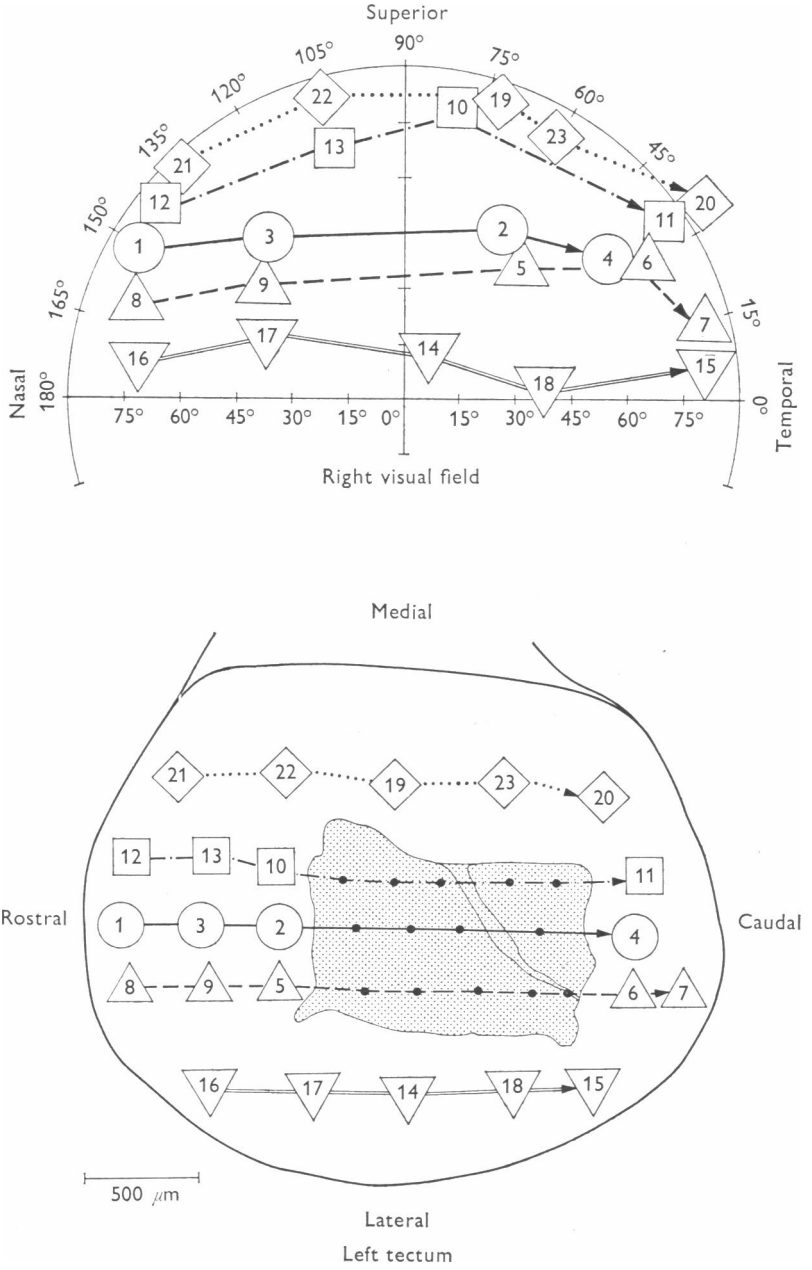
Retinal projection on tectal re-implants rotated 180°

Experiment 2. In thirty-four fish a rectangular piece of the tectal tissue was dissected out from near the centre of the left tectum, and then re-implanted to the same site after rotation by 180°. The optic nerves were left intact in all fish. Five fish died during recovery. Retinoetectal projections were mapped at two different periods after the 180° rotated tectal reimplantation. In the early period between 45 and 86 days, most of the tectal reimplants were found to have been revascularized and appeared to be healthy. It was impossible, however, to record any visual responses from the reimplanted tissue in twenty-one fish.

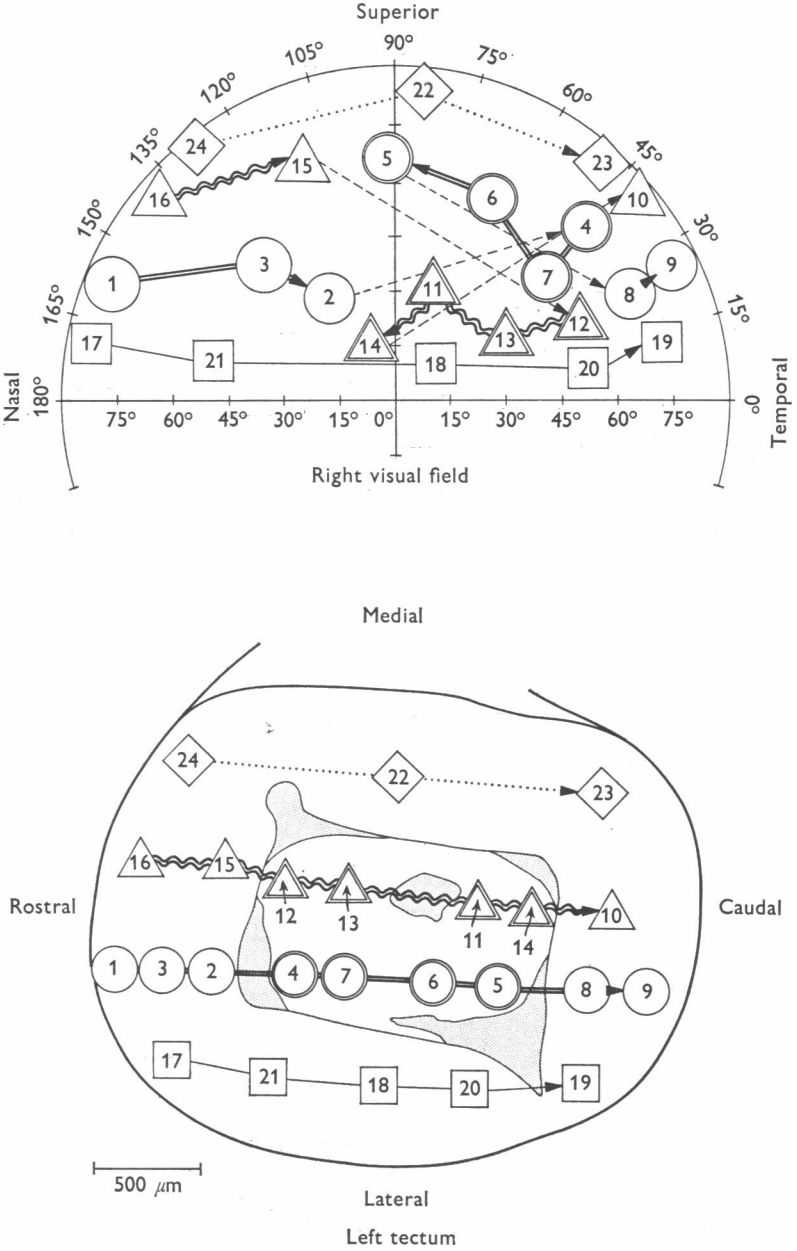
In the other eight fish, tested between 152 and 174 days after the tectal reimplantation, the grafted tectal tissue was found to be either missing or degenerated. Brisk visual responses were recorded, however, from the intact surrounding tectum. Text-fig. 2 shows a retinotectal projection map obtained 174 days after tectal reimplantation. The map indicates that the intact surrounding area of the tectum had acquired an orderly compressed visual projection from the whole retina following degeneration of the reimplant in conformance with previous findings in goldfish (Gaze & Sharma, 1970; Yoon, 1971, 1972*b*; Sharma, 1972).

About 6 months later the tectal surgery was repeated in another group of forty-two fish. The area of the tectal reimplant ranged from about one sixth to one fourth of the dorsal surface of the optic tectum. The optic nerves were left intact. Retinotectal projections were mapped at intervals between 64 and 385 days after the surgery. In the majority of the operated fish the reimplanted tectal tissue was found to have degenerated. In the case of five fish, however, the 180° rotated tectal reimplant had survived in place, and looked like an irregular island surrounded by large vacuoles along its sides near the central zone of the optic tectum (Pl. 1*d*).

The first neural responses to visual stimuli were obtained from the implant at 297 days after reimplantation. In two of the five fish only a small portion of the reimplanted area gave responses and it was impossible to construct a meaningful map. The other three fish yielded comprehensible and also consistent maps, one of which is shown in Text-fig. 3, obtained 385 days after reimplantation combined with 180° rotation. The map indicates that the visual projection from the part of the retina which innervated the 180° rotated tectal reimplant is organized in a completely reverse retinotopic order within the reimplanted area along both the rostrocaudal and the mediolateral axes of the tectum in contrast to the normal projection from the other part of the retina on to the intact surrounding area of the same optic tectum. The map shows an abrupt discontinuity in the location of corresponding receptive fields for pairs of



Text-fig. 2. Compression of the retinotectal projection following degeneration of the reimplanted tectal tissue. The map was obtained 174 days after the 180° rotated tectal reimplantation. The degenerated tectal reimplant is marked by the stippled area which gave no visual responses at all. The intact surrounding area of the tectum reacquired a compressed visual projection from the whole retina in correct retinotopic order.



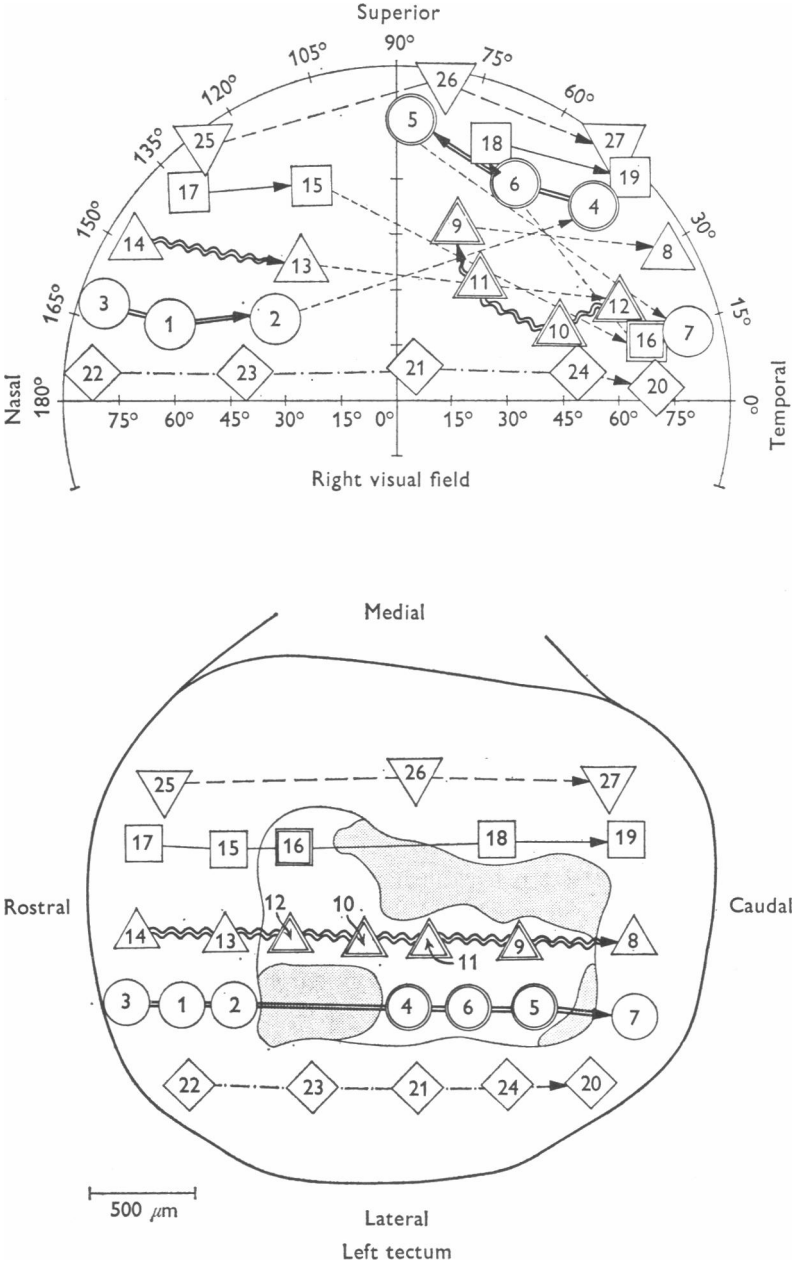
Text-fig. 3. Retention of the original topographic polarity by the 180° rotated tectal reimplant. The map was obtained 385 days after the reimplantation. The optic nerves were left intact. The stippled areas on the tectum represent vacuoles around the reimplanted tectal tissue. Tectal units recorded from the reimplanted area were marked by double-frame figures. Note that the corresponding receptive fields for these tectal units on the 180° rotated reimplant were distributed in a completely reverse topographical order in contrast to those for the tectal units recorded from the intact surrounding area of the same tectum.

adjacent tectal points no. 2 and no. 4; points no. 5 and no. 8; points no. 15 and no. 12; and points no. 14 and no. 10 in Text-fig. 3. Also note the adjacency in the location of corresponding receptive fields for pairs of remote tectal points no. 4 and no. 10; points no. 5 and no. 15; points no. 12 and no. 8; and points no. 14 and no. 2 in Text-fig. 3. The retinal area projecting on to the tectal reimplant shows a corresponding localized 180° rotation in its visual projection.

At the end of the neurophysiological mapping session, the brain of the same fish was preserved for histological examination. Pl. 2 shows sagittal sections of the same optic tectum. The over-all view of the optic tectum shows the 180° rotated tectal reimplant in the middle zone between the rostral and the caudal parts of the tectum (Pl. 2*a*). Note that the tectal reimplant is markedly thinner than the surrounding intact tectal layers. Bundles of regenerated optic fibres were found throughout the surviving area of the reimplanted tectal tissue (Pl. 2*b*). The cellular discontinuity between the rostral tectum and the tectal reimplant is shown in Pl. 2*c* and that between the reimplant and the caudal tectum in Pl. 2*d*. The regenerating optic fibres should have pierced through the gap (which may be as long as 100 μm in Pl. 2*c*) in search of their appropriate synaptic targets in the reimplanted tectal tissue. In spite of the atrophy and/or partial degeneration, however, the 180° rotated tectal reimplant was found to be able to form proper neural connexions with the regenerating optic fibres in a correct retinotopic order according to its original polarity in the topographical specification of its neural elements (Text-fig. 3).

Experiment 3. In forty-one fish tectal reimplants were rotated 180° as above and the contralateral optic nerve was also sectioned at the same time and allowed to regenerate.

Retinotectal projections were mapped at post-operative intervals of 92–374 days. Only two out of the forty-one operated fish yielded comprehensible and also consistent maps, one of which is shown in Text-fig. 4, obtained 374 days after operation. The reimplanted tectal tissue showed extensive partial degenerations as marked for the stippled areas on the optic tectum in the lower part of Text-fig. 4. In spite of the partial degeneration, however, the surviving area of the 180° rotated tectal reimplant was found to have retained its original topographic polarity: retinal projection on to the 180° rotated tectal reimplant is organized in a reverse retinotopic order along both the rostrocaudal and the mediolateral axes of the tectum in contrast to the normal projection on to the surrounding intact area of the same tectum (Text-fig. 4).



Text-fig. 4. Retinotectal projection map obtained 374 days after the 180° rotated tectal reimplantation and the optic nerve section. Tectal units recorded from the reimplant were marked by double-frame figures. Note that the corresponding receptive fields for these tectal units on the 180° rotated reimplant were distributed in a completely reverse topographic order in contrast to those for the tectal units recorded from the intact surrounding area of the same tectum. The stippled areas on the tectum represent vacuoles around the reimplanted tectal tissue.

DISCUSSION

The present experiments show that a part of the tectal tissue in adult goldfish may survive reimplantation on to the same optic tectum, and that the tectal reimplant eventually obtains synaptic connexions with appropriate optic fibres in consistent topographical order according to the orientation of the tectal reimplant. When the tectal tissue was reimplanted *in situ*, the restored visual projection showed a normal retinotopic order within the area of the tectal reimplant as well as over the other intact area of the tectum. If the tectal tissue was reimplanted after rotation by 180°, however, the visual projection from the part of the retina which innervated the 180° rotated tectal reimplant was found to be organized in a completely reverse retinotopic order within the reimplanted area along both the rostrocaudal and the mediolateral axes while the visual projection from the other area of the retina remained normal on the intact surrounding area of the same optic tectum. These results are compatible with preceding experiments by Sharma & Gaze (1971), involving 90° clockwise rotation of the tectal graft in adult goldfish. They reported that a consistent tendency for the rows of receptive field positions to deviate from the normal arrangements was found in the 90° clockwise rotated tectal graft such that receptive field positions near the horizontal meridian deviate towards the nasal edge of the visual field while those positions more dorsal in the visual field deviate in a temporal direction.

The results provide direct experimental evidence for Sperry's (1943*a*, 1963, 1965) hypothesis that not only the retina but also the optic tectum undergoes congruent topographical polarization during neurogenesis. Furthermore, the present experiments show that a piece of reimplanted tectal tissue retained its original polarity in spite of the fact that the tectal reimplant suffered an extensive partial degeneration around its margin and the layers of the surviving area of the reimplanted tissue underwent a severe atrophy. The critical minimum size of the tectal reimplant which retains the original topographic polarity may well be smaller than about one sixth of the dorsal area of the tectum. It is not known at what stage of embryonic development the optic tectum undergoes its initial topographic polarization. The fact that a piece of reimplanted tectal tissue retains its original topographic polarity regardless of whether it has been rotated or not indicates that the topographic polarization has become irreversible in the adult and persists even in a small fraction of rotated tectal tissue.

This irreversibility of the topographic polarity of the optic rectum is not incompatible with the plasticity of the optic tectum in readjusting size-disparity between the retina and the optic tectum in goldfish: it has been

found that a half-tectum may reacquire an orderly compressed visual projection from the whole retina following either ablation or separation of the other half of the tectum (Gaze & Sharma, 1970; Yoon, 1971). Furthermore, the compression of retinotectal projection in goldfish was found to be an experimentally reversible process which can be induced and then reinstated (Yoon, 1972*b*). The topographic order in the original connexions between the retina and the optic tectum, however, has been preserved in all readjustments involving compression, expansion, or transposition (Yoon, 1972*c*). In fact, the readjustments of neural connexions in compensating the size-disparity between the retina and the tectum always followed the direction imposed by the original topographic polarities of the retina and of the tectum.

The retention of original topographic polarity by a piece of reimplanted tectal tissue points out an important fact that the optic tectum is not a passive receiver of incoming optic fibres but an active accommodator which selects appropriate optic fibres to make proper synaptic connexions in a consistent topographic order. Therefore, the formation of neural connexions between the retina and the tectum should involve intercellular recognitions between the incoming optic fibres and the tectal neurones, presumably on the basis of their matching cytochemical affinities as proposed by Sperry (1943*a*, *b*, 1963, 1965) rather than it should be regarded as 'systems matching' as suggested by Gaze & Keating (1972). For example, the compression of retinotectal projection should involve more than just filling up the available space of the half-tectum by the whole optic fibres according to relative positions in their retinal origins. In order to accommodate the optic fibres from the whole retina, the half-tectum should have undergone regulative respecifications of the hypothetical synaptogenic intercellular affinity factors of its neural elements according to their new relative positions within the half-tectum along with the original topographic polarity of the half-tectum (Yoon, 1971, 1972*b*, *c*). In this context of the regulative neuronal respecification in accordance with the original topographic polarization, the neural connexions between the retina and the optic tectum in goldfish may be regarded to be in a dynamic equilibrium state rather than in a static, solid form.

I wish to thank Professor R. W. Sperry for his constructive criticism on the manuscript. The research was supported by U.S. Public Health Service Grant MH-03372 and the preparation of the manuscript was supported by Dalhousie Research Development Fund and Grant MA–4994 from the Medical Research Council of Canada.

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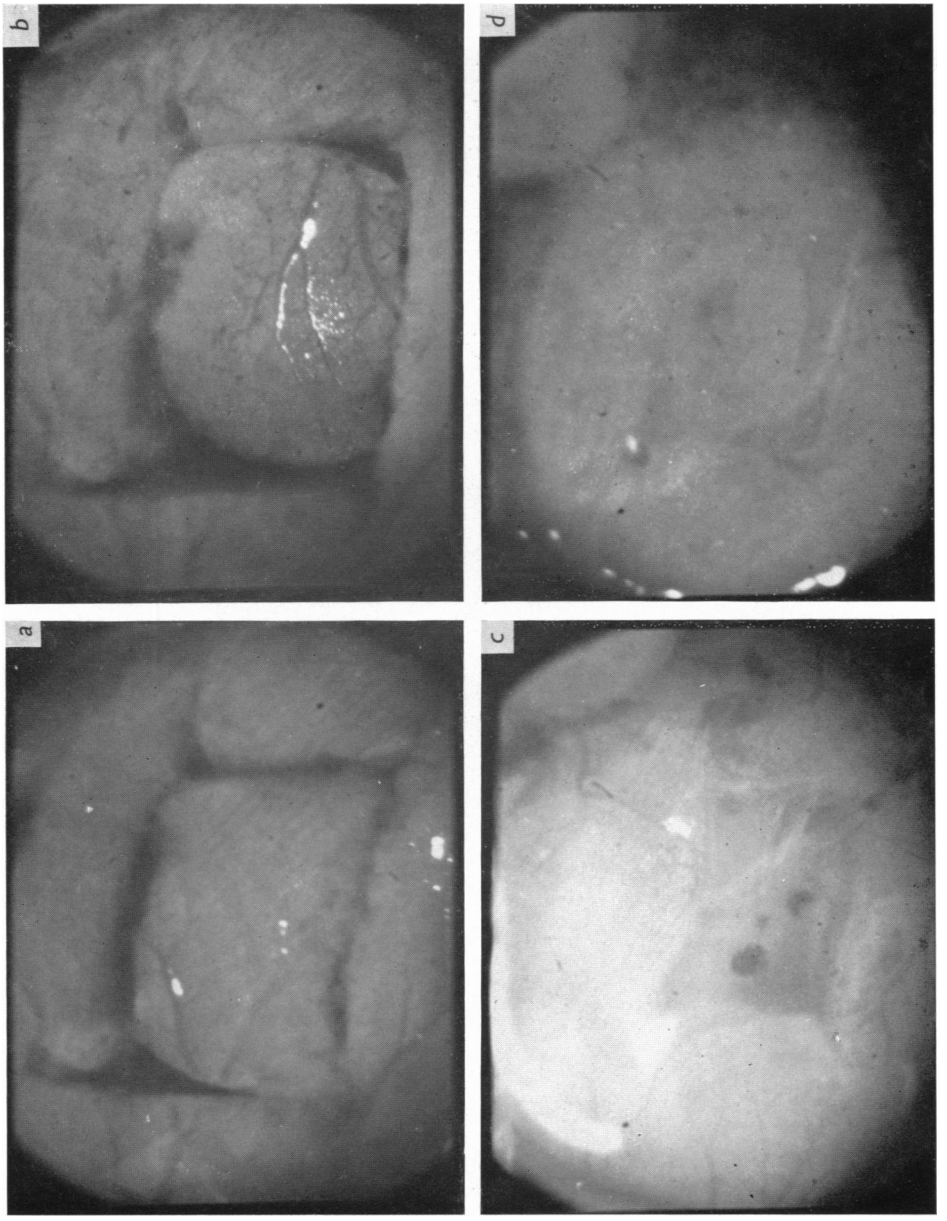
EXPLANATION OF PLATES

PLATE 1

Polaroid micrographs of the dorsal tectum (40 times): *a* shows a rectangular piece of the tectum which was dissected out from near the central zone of the tectum and then reimplanted to the same tectum *in situ*; *b* shows a piece of tectal tissue reimplanted to the same tectum after rotation by 180°; *c* shows a completely degenerated tectal reimplant, which left a hollow near the central zone of the tectum. In a few cases, large bundles of optic fibres were found to cross the hollow; *d* shows a tectal tissue which survived the 180° rotated reimplantation to the same tectum up to 385 days. Note the elongated vacuoles which surround the reimplanted tectal tissue.

PLATE 2

Micrographs of the sagittal section of the optic tectum with the 180° rotated tectal reimplant. The brain was fixed in Bodian fixative 385 days after the reimplantation, serially sectioned at 15 μm, and stained by the Bodian protargol method. R rostral, C caudal, D dorsal, V ventral. *a* Shows the over-all view of the optic tectum with the 180° rotated reimplant in the middle. Note that the reimplanted tectal tissue is markedly thinner than the surrounding intact tectal layers. *b* Shows the 180° rotated tectal reimplant at a higher magnification. Bundles of regenerated optic fibres are found throughout the surviving area of the reimplanted tectal tissue. The cellular discontinuity between the rostral tectum and the tectal reimplant is shown in *c*, and that between the reimplant and the caudal tectum in *d*.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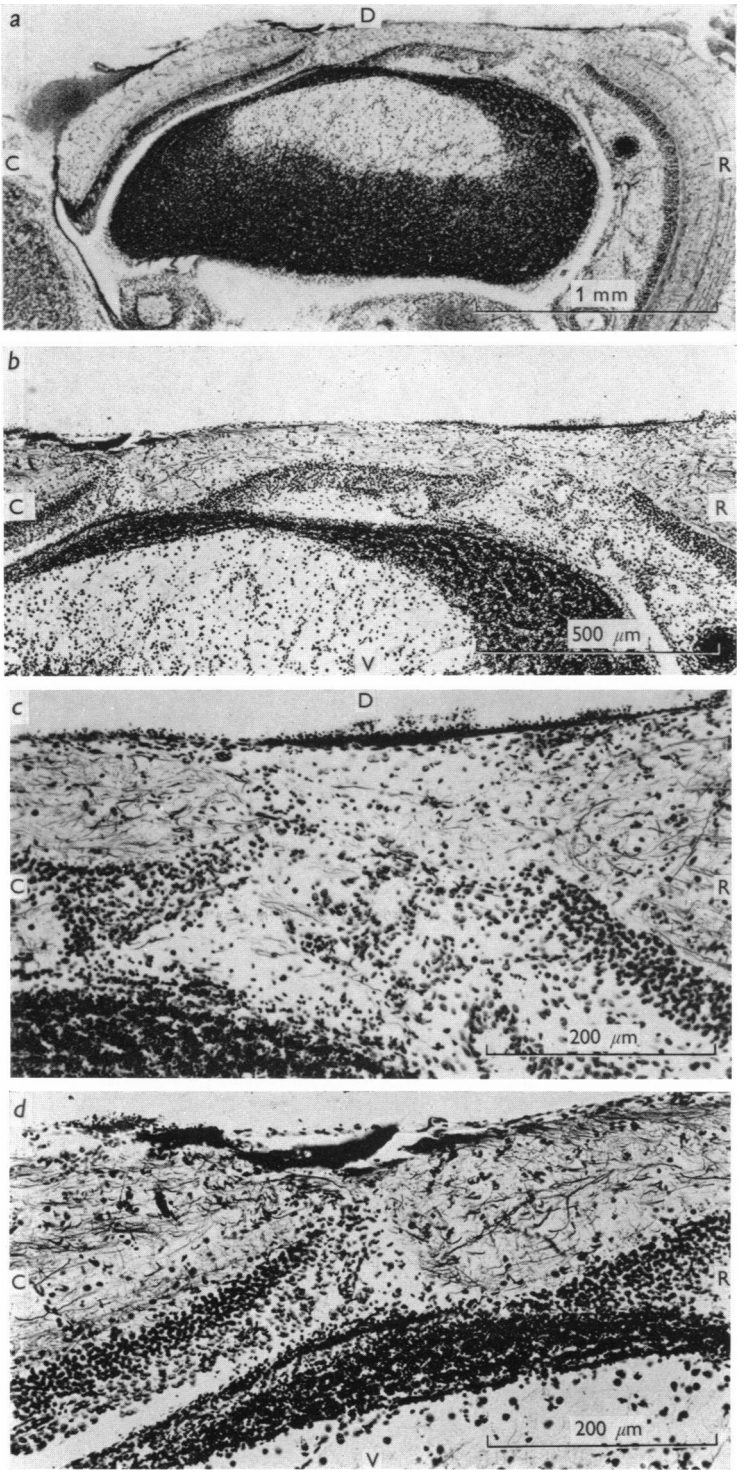
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